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SHORTER ARTICLES AND DISCUSSION

FURTHER REMARKS ON THE INHERITANCE OF CONGENITAL CATARACT

An article[1] by the writers in a previous number of this publication dealing with the inheritance of congenital cataract in a statistical way has been rather severely arraigned by Danforth[2] in a more recent issue. In our original paper we presented data taken from genealogical tables published by Harman in the " Treasury of Human Inheritance " which led us to believe—

1. That congenital cataract could no longer be considered as a single, dominant, unit character.
2. That Davenport should be criticized for making eugenical recommendations based on the inheritance of cataract as a dominant character when the method of inheritance is not positively known.
3. That from the evidence at hand cataract could better be considered as a single, recessive, unit character, reserving final decision as to this point until more complete data should become available.

Danforth believes with us that congenital cataract can not be considered as a simple, dominant character. Nevertheless he tries to defend Davenport from " unjust " criticism while he does not agree with him. It is upon the assumption of cataract as a positive or dominant character that Davenport bases his eugenical recommendation as follows:

> The usual method of inheritance is that of a positive character. Affected individuals have either half or all of their offspring affected, while two unaffected parents will probably not have defective offspring. However, as cataract usually appears late in life it is not always possible to predict whether the parent will become affected or not.
>
> The eugenic rule is this: If either parent has cataract at least half of the offspring will have it also. If a person belongs to a strain that has cataract but is free from it, advice must depend on the nature of the cataract. If in the family strain cataract appears early, before the age

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[1] Jones, D. F., and Mason, S. L., "Inheritance of Congenital Cataract," The American Naturalist, 50: 119–126, February, 1916.

[2] Danforth, C. H., "Inheritance of Congenital Cataract," The American Naturalist, 50: 442–448, July, 1916.

of the person who contemplates marriage, then such marriage may be advised; . . .[3]

As regards congenital cataract, then, Davenport advises that unaffected persons from affected stock can marry without fear of producing affected children. Harman's tables show over thirty matings of unaffected parents having at least one affected child.

No matter how unsatisfactory is the proof that cataract is a simple recessive, it should be borne in mind that the data given in Harman's tables do not stand the test when cataract is considered as a simple, dominant character. If the argument that heterozygous individuals sometimes show the recessive character is to be used to prove the dominance of cataract, it would be necessary to use the assumption to explain thirty-one exceptional families which have from one to eleven children of which 40 per cent. of the total are affected. On the recessive hypothesis there is only one exceptional family so far known to be explained. As long as it is not a simple dominant character it makes no difference whether it is a simple or complex recessive or a dominant governed by multiple factors, the eugenical recommendation quoted above should not be made, and we still believe that Davenport can be justly criticized.

Danforth objects to the disagreement between the observed and the expected results in our table I, giving the progenies of matings of normal by normal, and compares the goodness of fit unfavorably with data given by Usher on retinitis pigmentosa. In our results the disagreement lies in an excess of the actual number of affected children over the expected number. If, as Danforth says, "a certain number of congenital cataracts are produced by intrauterine poisoning without necessarily any reference to heredity" the tendency would be to raise the actual number of affected children above the expected. Also any cases of *origin de novo,* to which he believes we did not give enough consideration, would tend to have the same effect. Moreover, it should be noticed that Usher has over twice as many individuals to base his ratio upon, 320 as compared to 153 in our case.

Danforth states two main conditions which he says our assumption of cataract as a recessive character does not meet. The first is the low probability of an individual carrying the abnormality in a haploid or a diploid state meeting with a heterozygous normal, in random mating, which would be necessary to produce affected children. According to Danforth's calculations the probability of heterozygotes in the general population is one in thirty. He shows that Harman's tables give in some cases as high as eight out of nine individuals mating with normals and producing affected children, thereby showing that the normals are heterozygous on the recessive hypothesis. In the previous publication we did not give consideration to this point which is of noteworthy significance and we are indebted to the writer for calling our attention to it.

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[3] Davenport, C. B., "Heredity in Relation to Eugenics." Henry Holt and Co., New York, 1911, pp. 111–112.

This apparently high proportion of heterozygotes in the general population would be a serious objection to our simple recessive hypothesis if it were not for the fact that there is a considerable amount of consanguinity recorded in the pedigrees given by Harman. With each of the pedigrees including from one to many families there is a definite statement as to whether a record was made and, if so, whether or not consanguinity was present. Tabulating these statements shows that in sixty of the pedigrees no record was made. In twenty-four no consanguinity and in eleven consanguinity was definitely recorded. Then in those cases in which a record was made nearly 50 per cent. of the pedigrees show more or less intermarrying. Altogether there are seventeen cousin marriages.

With this amount of intermarrying among affected stocks the proportion of heterozygous individuals carrying the abnormality in a simplex condition would be greatly increased over the proportion in the general population, and Danforth's most serious objection to our hypothesis loses its force. Evidently no consideration was given to this point when he says "a more striking refutation of the assumption could hardly be found" (p. 447).

With regard to the second main condition which is raised against the assumption of cataract as a single, recessive, unit character Danforth seems to be partly in error, if we understand his statement correctly. He states: "If congenital cataract were recessive the normal children of a cataractous parent should themselves produce affected children in half as many cases as do their cataractous sibs, and the total number of affected children produced should be one half as great in the first case as in the second" (p. 446). Since on the recessive hypothesis only heterozygous normal and homozygous abnormal sibs are produced in equal numbers from matings of Nn × nn included in category B, and neither can produce affected children in turn, unless mated to a heterozygous normal or a recessive, we do not see why the normals should produce affected children in *half as many cases* as their cataractous sibs. If the chances for obtaining such mates were the same the number of matings which produce affected children should be approximately the same.[4]

The second part of the quotation is correct only when both normal and abnormal F_1 individuals have an equal chance to mate with individuals who are either affected or carry the abnormality in a recessive condition. The chances of the two classes mating with such individuals are probably not equal because individuals affected with cataract would have a harder time to find a mate than their normal brothers or sisters and there would be a greater tendency towards consanguineous marriages and consequently a greater chance of mating with cataractous individuals. The frequent intermarrying among affected stocks is well known with other abnormalities. Hence normal persons carrying the affectation in a heterozygous condition would be more likely to marry into unrelated stocks with a far less proportion of heterozygous individuals than would their affected sibs. If this is true then the expectation of the number of matings of affected F_1 individuals giving affected children in turn

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[4] In answer to a letter sent to Dr. Danforth asking about the above point the following was received which shows that we did not understand his meaning correctly:

In reply to your letter of September 29, I do not say in the paragraph to which you refer that of the children of cataractous parents half as many normal as cataractous *individuals* should produce affected offspring but, on the contrary, that the normals, taken as a group, should produce affected children ''in half as many cases'' (*i. e., at half as many births*) as do the cataractous. The families of *numerous individuals* in both groups would be expected to contain no cataractous individuals at all, but in those families (equal number for each group) where such children may occur there should be in the long run half as many cases in families with normal parents as in families with one cataractous parent. The remainder of the paragraph to which you refer and the statements in your letter show, I think, that we are in complete agreement as to the theoretical expectations; it was my unfortunate use of the word ''cases'' which no doubt caused you to raise the question. I meant it to refer to F_3, you doubtless suspected it might refer to F_2. This suspicion was undoubtedly strengthened by my ''relation of one to two'' which is one of those slips of the pen for which I have no means of accounting. Of course it should have been ''one to one'' and that fact was uppermost in my mind at the time of writing the passage!

would be greater than that of the unaffected and the total number of children would therefore be more than twice as great.

Danforth, however, after raising this condition does not determine the number of affected children from the affected and unaffected F_1 individuals, but calculates the percentages of these two classes of parents which produce at least one affected child. He finds that eighty-six per cent. of the cataractous children of a cataractous parent themselves produce some affected children and thus presumably have mated with heterozygous normals. Of the normal children from the same F_1 generation only ten per cent. produce affected children. If the chances for securing similar mates were the same these percentages should be approximately equal. The relation of ten to eighty-six which does not conform to a one to two ratio as Danforth states that it should necessarily deviates still more widely from a one to one ratio.

There are two reasons why this deviation from a one to one ratio can be expected in favor of a larger number of affected matings giving affected children than of unaffected matings. The first lies in the fact that matings of affected by heterozygous normals should give a one to one ratio of affected and normal children, whereas the matings of heterozygote by heterozygote should give a ratio of one to three. As was emphasized in our previous publication the only criterion by which it can be determined whether the mates to the two kinds of F_1 individuals are heterozygotes or homozygotes is the production of at least one affected child. In families with a small number of children the matings which promise a one to one ratio would have a greater chance of producing at least one affected child than matings which promise a ratio of one affected to three unaffected children. Hence more of the families of the latter than of the former class would be omitted from the data.

The other reason why the deviation that Danforth obtains can be expected is that which has already been mentioned, namely, that affected individuals are more likely to marry related individuals because of the greater difficulty of obtaining a mate than the unaffected would have. The proportion of heterozygotes in *affected strains would be far higher than in the general population*, so that the chances of the two kinds of F_1 individuals mating with a heterozygous normal would not be equal as Danforth considers them to be.

It is recognized that these arguments are extremely indefinite and that it is difficult to determine just how much value to give them. They are however hardly necessary since the numbers ninety-six and forty-seven upon which Danforth bases his criticism are too small to make a really critical comparison.

Since the number of affected F_1 individuals which should give one half affected children exceeds the number of unaffected F_1 individuals which should have only one third affected children, the actual number of affected children in the two kinds of F_2 populations would deviate proportionally farther from a ratio of one to two. If it is conceded that the chances for the two kinds of matings are not equal, then this deviation would be expected.

The three cases in category C which we gave as matings of abnormal by abnormal which theoretically should give only abnormal children according to the simple recessive hypothesis can be found in Harman's tables in the "Treasury of Human Inheritance"[5] as follows: Table 309, Parents I, 1 and 2—Children II, 1 to 5; Table 312, Parents II, 3 and 5—Children III, 3 to 4; and Table 342, Parents III, 28 and 37—Children IV, 60 to 66. Danforth says that he can find only two of these. They are probably 309 and 342. The one which occurs in Table 312 should not have been used without an explanation. Although the chart indicates that both parents are affected as well as their two children, the description of the family shows that the exact parentage is somewhat in doubt. It was an error on our part not to mention this fact.

With regard to the family in 342 in which part of the children are normal where only abnormals are expected, Danforth does not accept our explanation that heterozygotes sometimes have the recessive character. This is quite frequently shown in other material. His refusal to accept this explanation to account for the one exception to the recessive hypothesis is shown in the following quotation: "a single bona fide case in which two affected individuals produce normal offspring is sufficient to overthrow it" (the recessive hypothesis) (p. 447). We can not understand his refusal to accept this explanation to account for one exception when he is willing to use it to explain thirty-one exceptions to the dominant hypothesis! This is evident from the following quotation previously alluded to:

> Again, since Jones and Mason elsewhere in the same paper (p. 124)

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[5] Harman, N. B., "Treasury of Human Inheritance," Eugenic Laboratory Memoirs, XI, Part 4, Section XIIIa, pp. 126–169, Pl. XXVIII–XXXIII, Dulau and Co., London, 1910.

use the same argument that "heterozygous individuals sometimes show the recessive character," we might, if necessary, use the same argument to prove the dominance of cataract. On the assumption that congenital cataract is dominant instead of recessive it might be maintained that in those cases where both parents of affected individuals seem to be normal, one of them is, after all, heterozygous—and affected children are therefore to be expected (p. 444).

Perhaps Danforth would be willing to consider another explanation which he suggests, that somatic cataracts of a congenital origin are not uncommon. If one of the parents in question had a somatic cataract the appearance of normal children would be expected but not of affected children unless the parent was also heterozygous for hereditary cataract. A probability which would be rather remote but not impossible.

From the data as they have been gathered up to this time it seems impossible to arrive at an explanation of the mode of inheritance of cataract which will be entirely satisfactory. While more proof is awaited, we believe that the assumption of congenital cataract as a single, recessive, unit character has the best support from the facts at hand. The article by Danforth has brought out several important considerations which we neglected. It is regretted that in this paper which at first sight makes out a strong case against our recessive hypothesis there is nothing offered towards a different solution of the problem.

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THE STATUS OF FOWLER'S TOAD, *BUFO FOWLERI* PUTNAM

S. P. Fowler, of Danvers, Essex County, Massachusetts, appears to have been the first to recognize the fact that this toad differed in many respects from the common toad. In a letter[1] to Prof. F. W. Putnam, Fowler gave a very accurate and complete account of the song and habits of this toad as he had observed it around Danvers.

Cope (see loc. cit.) discussed in much detail *Bufo lentiginosus fowleri* (Putnam). Little was known of this toad at the time Cope wrote. In fact, Cope stated that it was confined to a few

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[1] Cope, E. D., "The Batrachia of North America," Bull. 34, U. S. National Museum, 1889, pp. 279–281.